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BY

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SLUGS AS MYCOPHAGISTS.

By Professor A. H. R. Buller, D.Sc., Ph.D., F.R.S.C.

INTRODUCTION.

Slugs eat many fleshy fungi; and in woods and gardens one can often find fruit-bodies which have been more or less damaged by these animals. Fungi, therefore, especially in certain localities and in certain seasons, must be considered as an important source of slug food. Among the fungi which slugs attack may be mentioned: species of *Amanita*, *Pleurotus*, *Russula*, *Psalliota*, *Coprinus*, *Boletus*, *Polyporus* and *Phallus*. Leathery fungi, e.g. *Polystictus versicolor*, *Stereum hirsutum* and *Schizophyllum commune*, and gelatinous fungi, e.g. *Hirneola auricula-Judae* and *Auricularia mesenterica*, are generally avoided*.

A fruit-body which has been partially eaten by a slug can be easily recognised: (1) by the peculiar manner in which it has been rasped and mined, and (2) by the slug's slime tracks. Slugs are nocturnal animals. During the day, they hide under soil or in dark crevices; but, as darkness comes on, they emerge from their places of concealment and seek their food. They therefore visit the fruit-bodies of fungi during the night, but, as a rule, retire from them with the advent of day. Sometimes, however, a slug which has made a hole on the under side of the pileus or in the top of the upper part of the stipe of a large agaric, such as *Boletus luteus* or *Lactarius piperatus*, remains half-hidden in the hole throughout the day and then may be found by the observer.

SLUG-DAMAGED FUNGI IN AN ENGLISH WOOD.

On September 8, 1920, accompanied by Mr W. B. Grove, I spent an afternoon in a wood at Earlswood, near Birmingham, England, investigating the damage which the slugs had done to the fungi. Out of several hundreds of fruit-bodies of fleshy Hymenomycetes observed, I found very few which had not been visited and partially eaten by slugs. Some of the fruit-bodies had been absolutely ruined by these animals. Thus the stipe of a large *Boletus flavus* had been eaten in two; and the separated pileus had completely lost all its hymenial tubes, whilst the pileus-flesh had become reduced to a thin perforated shell. A slug was found ensconced in one of the cavities of the flesh; and, doubtless, it was only waiting for the night to sate its voracious appetite once more upon the wreck to which it was

* A few experiments upon the edibility of fungi for slugs are recorded in my *Researches on Fungi*, I, 1909, p. 229.

clinging. Some other fruit-bodies, e.g. *Russula ochroleuca*, *Lactarius piperatus* and *L. turpis*, were almost equally damaged. The following species were found to have been visited and partially eaten by slugs:

Species attacked by Slugs.

<i>Amanita rubescens.</i>	<i>Laccaria laccata.</i>
<i>Amanitopsis vaginata.</i>	<i>Hypholoma fasciculare.</i>
<i>Clitocybe clavipes.</i>	<i>H. sublateritium.</i>
<i>Russula emetica.</i>	<i>Flammula sapinea.</i>
<i>R. ochroleuca.</i>	<i>Paxillus involutus.</i>
<i>R. sardonia.</i>	<i>Cortinarius anomalus.</i>
<i>R. heterophylla.</i>	<i>C. paleaceus.</i>
<i>R. nigricans.</i>	<i>C. caninus.</i>
<i>R. adusta.</i>	<i>C. rigidus.</i>
<i>Lactarius piperatus.</i>	<i>Boletus flavus.</i>
<i>L. subdulcis.</i>	<i>B. chrysenteron.</i>
<i>L. glycosmus.</i>	<i>B. scaber.</i>
<i>L. turpis.</i>	<i>Clavaria cinerea.</i>

The following species were found not to have been eaten by slugs:

Species not attacked by Slugs.

<i>Lactarius quietus.</i>	<i>Inocybe geophylla.</i>
<i>L. rufus.</i>	<i>Tubaria furfuracea.</i>
<i>Collybia butyracea.</i>	<i>Cortinarius sanguineus.</i>
<i>Flammula inopus.</i>	<i>Polystictus versicolor.</i>
<i>Inocybe asterospora.</i>	<i>Lycoperdon pyriforme.</i>

Of the species attacked, some, e.g. the *Russulae*, were damaged much more than others. Scarcely a single fruit-body of any species of *Russula* could be found which had not been partially eaten. Very few of the fruit-bodies of *Hypholoma fasciculare*, *Laccaria laccata* and *Lactarius glycosmus* had been eaten and these only slightly, so that it seems that slugs do not much relish these species.

Of the species not attacked by slugs only single fruit-bodies were found of *Flammula inopus*, *Inocybe asterospora* and *Cortinarius sanguineus*, and a few fruit-bodies only of the relatively tiny *Inocybe geophylla* and *Tubaria furfuracea*, so that it is possible that, if the fruit-bodies of these fungi had been more numerous, some of them might have been found attacked. The species which seemed to have been definitely avoided by slugs were *Lactarius quietus*, *L. rufus*, *Collybia butyracea*, *Polystictus versicolor* and *Lycoperdon pyriforme**

Two species of slugs were found upon the fungi, a larger

* These five species are also distasteful to human beings.

reddish one about one inch long and a smaller darker one. Mr P. T. Deakin kindly identified the former as *Arion subfuscus* var. *aurantiaca* and the latter as a *Limax*. The specimens submitted for the *Limax* were too immature for exact identification.

Polystictus versicolor, *Stereum hirsutum*, and other tough and leathery fungi, are probably protected against the ravages of slugs by their physical consistence; while *Lactarius quietus*, *L. rufus*, *L. glyciosmus*, *Collybia butyracea*, *Laccaria laccata* and *Lycoperdon pyriforme* are more or less protected against slugs by their chemical contents. The majority of fleshy fungi, however, seem to be in no way protected against slugs, and some of the commonest species, e.g. those of *Russula*, *Amanita*, *Amanitopsis* and *Boletus*, often suffer most. On the whole, the very soft-fleshed species seem to be the most relished by slugs, and these animals are particularly fond of the soft parenchymatous tissues of the *Lactarii* and of the soft hymenial tubes and flesh of many *Boleti*. Voglino has supposed that slugs are important agents in bringing about the dissemination and germination of the spores of *Russulæ*, etc., and is inclined to believe in the existence of symbiotic relations between slugs and *Hymenomycetes**. I am rather of the opinion that, when a slug attacks a fruit-body, the advantage is chiefly, if not entirely, on the side of the slug and that, from the point of view of the fungus, the slug is a troublesome ectoparasite. As I have pointed out elsewhere, the fruit-bodies of the *Hymenomycetes* are beautifully organised to secure the dissemination of the spores by the wind and their injury by slugs certainly prevents a great many spores from being liberated†.

ABSENCE OF SLUGS FROM A WOOD IN CENTRAL CANADA.

In the late autumn of 1920, I spent several days at Kenora on the Lake of the Woods, central Canada, studying the fleshy fungi in the woods; and, although I made a careful search, I could not find a single agaric damaged by a slug.

Slugs, which are common in England and in the extreme west of Canada (British Columbia), where the climate is damp and moderately warm, are rare in central Canada, where the climate is very dry and relatively cold. Most native-born Manitobans, so far as I can find out by enquiry, have never seen a living slug; and there can be no doubt that the big species of *Limax*, *Arion*, etc., which abound in gardens and woods in England, are entirely absent from central Canada. Nevertheless, Mr J. W. Wallis of Winnipeg has assured me that he once found some small slugs living wild in the open in Manitoba; and I, myself,

* Cf. my *Researches on Fungi*, 1, 1909, pp. 226-227.
† *Ibid.* p. 228.

have seen one small slug in a greenhouse at Winnipeg. However, I have never yet seen a slug in any of the woods of central Canada.

Since fleshy fungi, e.g. Russulæ, Lactarii, Amanitæ, Cortinarii, etc., occur in great variety and numbers in the woods of central Canada, and since slugs do not occur in these woods or are very rare there, it seems safe to infer that fleshy fungi, such as Russulæ, Lactarii, Amanitæ, Cortinarii, etc., in no way depend upon slugs for the dissemination or germination of their spores.

SOME CONCLUSIONS.

We may conclude from the above observations: (1) that slugs, under natural conditions, may attack and feed upon most species of fleshy Hymenomycetes occurring in woods, (2) that the attacks of the slugs often seriously interfere with the production and liberation of spores by individual fruit-bodies, (3) that most species of fleshy fungi are in no way protected against slugs, and (4) that very many species of fleshy fungi do not depend upon slugs for the dissemination or germination of their spores.

* THE FINDING OF FUNGI BY SLUGS.

Before eating a fungus, a slug must first find it. Now, according to zoologists, the common slugs of English fields and woods, e.g. *Limax maximus* and *Arion ater*, although possessing eyes, can see clearly for a distance of only 1 or 2 mm. and find their food chiefly by their sense of smell*. We must therefore suppose that slugs find the fungi upon which they feed chemotactically, i.e. by changing their direction of locomotion in response to the chemical stimulus arising from the odoriferous substances which the fungi give off.

PREVIOUS CHEMOTACTIC EXPERIMENTS.

As evidence that slugs find their food by their sense of smell A. H. Cooke cites the following observations†:

"M. Parenteau was one day walking along a dusty high-road, when he noticed, near the middle of the road, an empty bean-pod and two Arions eating it. Attributing the meeting of feeders and food to mere chance, he was walking on when he noticed a second bean-pod, and, about two yards away from it, a third Arion, hurrying straight towards it. When the Arion had yet

* V. Willem, Arch. Biol. XII, 1892, p. 57, cited from A. H. Cooke, Cambridge Natural History, Molluscs, 1895, p. 185.

† A. H. Cooke, Cambridge Natural History, Molluscs, 1895, pp. 193-194. These observations were first recorded by Moquin-Tandon in his Mollusques de France, I, p. 130.

more than a yard to traverse, M. Parenteau picked up the bean and put it in his pocket. The Arion stopped, raised its head, and turned in every direction, waving its tentacles, but without advancing. M. Parenteau then carried the bean to the other side of the road, and put it in a small hole behind a piece of stone. The Arion, after a moment's indecision, started off straight for the bean. Again the position of the precious morsel was changed, and again the Arion made for it, this time without being further tantalised.

M. Moquin-Tandon noticed, one rainy day in the botanical gardens at Toulouse, two *Limax maximus* approaching a rotten apple from different directions. He changed the position of the apple several times, placing it at a sufficient distance to be sure they could not see it, but they always hit it off correctly, after raising their heads and moving their long tentacles in every direction. It then occurred to him to hold the apple in the air, some centimetres above the head of the *Limax*. They perceived where it was, raised their heads and lengthened their necks, endeavouring to find some solid body on which to climb to their food."

As confirming M. Moquin-Tandon's experiment, and as further evidence that the olfactory sense in *Limaces* is extremely acute, J. W. Taylor in his Monograph relates the following*:

"Mr L. E. Adams, about ten o'clock, one dark, windy, and wet evening in August, 1897, at Clifton, Derbyshire, saw a *Limax maximus* crawling directly toward a plate upon the lawn, containing the remains of the dog's dinner; when first observed the slug was about six feet distant from the plate, but within thirty minutes had reached it; the plate was then removed to a second position, about six feet away, but in another direction; the slug almost immediately changed its course, and again made straight towards the plate, on again nearing it the same process was repeated with the same result, the plate being finally removed and placed in a fourth position, eight feet away, and directly to the leeward of the slug, yet in a little more than half-an-hour the slug had reached the plate."

Ernst Stahl† of Jena, whilst carrying out some extended investigations upon the chemical and physical means by which certain plants are protected from the attacks of slugs and snails, incidentally convinced himself by experiment that slugs find their way to their food by their sense of smell. He placed a

* John W. Taylor, Monograph of the Land and Freshwater Mollusca of the British Isles (Testacellidae, Limacidae, Arionidae), Leeds, 1907, p. 37.

† Ernst Stahl, Pflanzen und Schnecken, Eine biologische Studie über die Schutzmittel der Pflanzen gegen Schneckenfrass, Jena, 1888, pp. 15-16, footnote.

slug (*Limax*) upon a moistened dinner plate and with his mouth blew gently upon it in a horizontal direction. He found that the current of air so produced had no particular effect upon the slug's movements. He then put a cup fungus, *Peziza vesiculosa*, between his mouth and the slug and continued blowing. The slug then immediately changed its behaviour. If the slug's head had been turned away from the experimenter, the slug raised it, moved its tentacles about in the air, soon turned the front part of its body round, and then steered, as the blowing continued, straight toward the fungus. That the slug sought its food by its sense of smell and not by its sense of sight, Stahl showed as follows. He blew over the *Peziza* as before and waited until the slug had approached to within about 1 cm. of its surface. He then took another *Peziza*, placed it upon the opposite side of the plate, and blew over it toward the slug. The new current of air was thus made to move in the opposite direction to the first one and to pass over the second fungus, the slug, and the first fungus successively. Stahl then observed several times that the slug, although only 1 cm. away from the first fungus and many cm. away from the second, turned round, left the near-by first fungus, and crawled directly toward the distant second one from which the current of air was coming. It was only when the slug was almost touching the first fungus that Stahl was unsuccessful in trying to induce the slug to turn round and seek the second.

NEW CHEMOTACTIC EXPERIMENTS.

With a view to testing the supposition that slugs find their food, and in particular find fungi, by their sense of smell, I have made a series of experiments, under conditions as natural as possible, upon the attraction of *Limax maximus* to *Phallus impudicus* and to certain Hymenomycetes. Before giving an account of these experiments, however, it will be necessary for me to make a few preliminary remarks upon both the *Limax* and the *Phallus*.

According to Simroth and Scharff, the food of *Limax maximus* consists of non-chlorophyllaceous substances, while anything containing chlorophyll is as a rule refused*; and W. A. Gain considers *Limax maximus* a very dainty feeder, preferring fungi to all other foods†. Stahl‡ divided slugs and snails into *omnivora* and *specialists* and states that *Limax maximus* is a specialist which feeds chiefly on fungi.

Limax maximus, like most other slugs, hides during the day in crevices under stones or in the soil, and only emerges from its

* A. H. Cooke, *loc. cit.* p. 31.

† *Ibid.* p. 32.

‡ E. Stahl, *loc. cit.* p. 15.

place of retreat as darkness is coming on. It was therefore necessary for me to make my experiments during the evening and night. Slugs and snails possess to a considerable degree the power of *homing*, i.e. of returning to the same hiding place day after day, after their night excursions in search of food*. My observations have convinced me that *Limax maximus* is a homing slug. The slugs used in my experiment had a fixed abode to which they always returned after their nocturnal peregrinations; and the realisation of this fact was of considerable help to me in suitably arranging the position of the fungus fruit-bodies which I wished the slugs to visit.

It has been calculated that an average-sized snail of moderate pace progresses at the rate of about a mile in 16 days and 14 hours†. This works out at about 13.3 ft. per hour. The rate of movement of *Limax maximus* is probably not very different from that of a snail. On one occasion I found that a *Limax maximus* had travelled from one point to another 12 ft. distant in 1 hour and 20 minutes; but the course taken was not the shortest possible, so that I have no doubt that the actual pace of the slug somewhat exceeded 10 ft. an hour.

Phallus impudicus—the Stink-horn Fungus—as every botanist is aware, is one of the most remarkable of all fungi. The young fruit-body—sometimes known as a Devil's Egg—is a soft spherical white ball, a little larger than a hen's egg; and it is protected upon its exterior by a thick gelatinous peridium. At maturity, the ball suddenly bursts at the top, and then there emerges from it in the course of about half-an-hour a sort of Jack-in-the-Box made up of a long, white, hollow, spongy, bread-like stipe bearing at its free end a conical cap covered with dark green slime. The slime contains sugar and millions of green spores, and from it issues a very powerful and offensive odour. Dung flies are attracted to the fungus by the smell, alight upon the green cap, lick up the sweet slime, and carry away the spores upon their straggling legs and inquisitive proboscides and within their alimentary canals. Thus the spores of the fungi are disseminated through the agency of insects.

The smell from the cap of an expanded *Phallus impudicus* attracts not only flies during the day but also slugs during the night. Early in the morning I have several times found an expanded fruit-body with a stipe which had been half-eaten by slugs during the previous night, the slime left upon the fungus and the nature of the damage affording a clear indication of the identity of the marauders; and, in the twilight of the evening, I have sometimes found a slug, *Limax maximus*, actually upon a *Phallus* engaged in feeding.

* A. H. Cooke, *loc. cit.* pp. 34-36.

† *Ibid.* p. 46.

Experiment I. At my father's house at Birmingham, England, there is a smooth, well-compressed, gravel carriage-way which is oval in form, 40 ft. wide and 60 ft. long. On a border, at the edge of the gravelled area, one evening in August as darkness was setting in, I found an expanded Phallus upon which a slug, *Limax maximus*, was feeding. I removed the slug and set the fungus upon the gravel at a distance of 10 ft. from the edge of the border. The next morning I found that a slug had visited the fungus upon the gravel, and the slime-track revealed that the slug had come from the border where I had first found the fungus with a slug feeding upon it. The track was very direct from the border to the fungus. It therefore appeared that the Phallus had attracted the slug chemotactically for a distance of at least 10 ft.

Experiment II. Shortly after making the above experiment, on August 28, 1920, I visited Sutton Park, Warwickshire, and there procured nine large Phallus balls from under a Holly bush. The balls were full-grown, but still quite odourless; and their stipes were beginning to elongate, for I could feel them in some of the balls pressing upwards against the top of the peridium. I took the balls home to my father's garden, planted them in damp soil in pots, and set the pots in the greenhouse. Two days afterwards, one of the balls opened and a tall stipe covered with a strongly odorous dark-green cap emerged. In the evening I set the expanded Phallus in the middle of the gravelled area. Next morning I found that the fungus had been visited by a slug which, as indicated by its slime-track, had crept over the gravel for a distance of about 21 ft.

Experiment III. The other Phallus fruit-bodies opened one by one, and with them I made several other experiments like the one just described. In one of them a slug came at night about 24 ft. over the gravel to two fruit-bodies which were in one pot, ate a piece out of each of the two stipes, and then crept between the bottom of the pot and the gravel. When I raised the pot in the morning, in order to take it to a place where the Bluebottle flies could not eat up all the green slime, I found the slug beneath. The slug was kindly identified for me by Mr P. T. Deakin as *Limax maximus* var. *obscura*.

On three other nights I placed pots with expanded Phallus fruit-bodies in the middle of the gravelled area, but no slugs visited them. This may have been due in part to the paucity of slugs in the borders and in part to the weather being rainy and windy. The successful experiments were performed on still nights. Slime tracks were only found in the morning upon the gravel when a slug had visited a Phallus during the previous night.

The above observations show that *Limax maximus*, under natural conditions, guided by its sense of smell, sometimes travels from 21 to 24 ft. toward an expanded fruit-body of *Phallus impudicus* and that, upon coming in contact with the fruit-body, it feeds upon the stipe.

I employed *Phallus impudicus* for my first experiments upon the chemotaxis of slugs because of its very powerful odour and the convenience with which I could procure and handle its fruit-bodies; but I have found that similar experiments can be performed with *Boleti* and *Agaricineae*.

Experiment IV. On September 8, I procured three fresh fruit-bodies of *Boletus scaber* from a wood and, in the evening of September 9, placed them upon the gravelled area at a distance of 10 ft. from the border. During the night a slug came from the border across the gravel to the fruit-bodies and ate three holes in the top of one of the pilei. A similar experiment made at the same time with a large fruit-body of *Russula heterophylla* was also successful.

Experiment V. The next evening, September 10, about 8 p.m., I placed upon the gravel three little heaps of hymenomycetous fruit-bodies. In the first heap were the three fruit-bodies of *Boletus scaber* which had been used the night before, in the second three fruit-bodies of *Cortinarius caninus*, and in the third three fruit-bodies of *Russula nigricans*. Each heap was made at a distance of 12 ft. from the border and the three heaps were in a row, the central heap being that of *Boletus scaber* and the intervals between the heaps being 4 ft. Having had considerable difficulty in some of the previous experiments in tracking the slime-trail upon the gravel owing to the intermittency or thinness of the trail and owing to the effects of dew, I placed some large fern leaves in a line along the edge of the gravel by the border, so that, if a slug crossed the line, it would leave a trail behind which could be easily detected. The night was a very dark one. About 10 p.m. I went out with a lighted taper to see what was happening. On examining the fern leaves I found upon the leaflets a shinging slime-trail, the direction of which proved that the fern line had already been crossed by a slug. I then hunted about on the gravel and found the slug, a *Limax maximus*, about 4 inches long, actually on its way to the fungi. The slug was already 4 ft. from the border whence it had come and was heading in the right direction to reach the row of fungus heaps some 8 ft. distant. I noticed, however, that the path of approach to the fungi was by no means a straight line but was made up of a series of curves. At 10.45 p.m. I found the slug about 4 ft. from two of the heaps of fungi, and at 11.20 p.m. I found the slug actually upon one of the fruit-

bodies of *Boletus scaber* quietly feeding. No other slug could be seen anywhere. The next morning I detected the slime-trail of the slug in the neighbourhood of the heap of Boleti but nowhere else, the trail having been weakened or destroyed by dew formation; and the slug had disappeared. In all probability the slug had returned to the border whence it had originally come.

Experiment VI. The next evening, September 11, I set out upon the gravel the same three heaps of fruit-bodies as had been used the night before. Again the heaps were made in a row parallel to the edge of the border, the intervals between the heaps being 4 ft., the *Boletus scaber* heap occupying the central position in the row and the *Cortinarius caninus* and *Russula nigricans* heaps the end positions. However, the arrangement of the heaps differed from that of the night before in that each heap instead of being only 12 ft. from the edge of the border was now 20 ft. The condition of the *Russula nigricans* and *Cortinarius caninus* fruit-bodies was still good, but the *Boletus scaber* fruit-bodies were now in an advanced stage of putrescence. The evil state of the *Boletus scaber* fruit-bodies was perhaps the reason why, as we shall see in the sequel, they were not visited by a slug in this particular experiment. The night was again very dark and still. At 9.40 p.m., with the help of a lighted taper, I found a *Limax maximus* which had just emerged from its hiding place and which was moving behind a block of sand-stone in the border 21 ft. from the fungi. At 11 p.m. I went out again and found that the slug had already travelled 11 ft. upon the gravel toward the fungi from which it was now only 9 ft. distant. I watched the slug for a little time but, being afraid of disturbing it too much, soon retired into the house. At 12 p.m. I sought the slug again and found it 6.5 ft. away from the row of fungi; but, to my surprise, it was moving away from the row of fungi instead of toward it. At 1 a.m., the slug was 5 ft. away from each of the heaps of *Boletus scaber* and of *Russula nigricans*; at 1.30 a.m., about 2 ft. away; and, finally, at 2 a.m., actually upon one of the fruit-bodies of *Russula nigricans* devouring the gills. Thus the slug, after some five hours of wandering, had at last succeeded in finding one of the heaps of fungi set 20 ft. from the edge of the border where the slug had first been seen.

The slug, between 9.40 p.m. and 11 p.m., must have travelled almost directly toward the fungi; for, during this period, it traversed 1 ft. of border and 11 ft. of gravel in the direct line of its journey. But between 11 p.m. and 1 a.m. this rapid progress was not kept up and there was a great waste of time, for during this period the net advance of the slug toward the fungi

was only 4 ft. The slug, as the track showed the next morning, seems, during these two hours, to have wandered more or less round and round in a knotted manner as if it had had some difficulty in detecting the scent of the fungi. As it happened, the slug was obliged to cross the line where the heaps of fungi had lain during the previous night and day, and it is therefore possible that the fungi had in some way scented the ground and that the scent had mis-led the slug. It is also possible that variations in air currents took place in such a way as to send the odour of the fungi in the heaps toward the slug only very intermittently. But, whatever may be the true explanation, it is certain that between 11 p.m. and 1 a.m. the slug lost much time and spent a considerable amount of energy in fruitless wandering.

There was nothing upon the gravel for the slug to eat except the fungi I had placed there and, if the slug had continued in the direction in which it set out without finding the fungi, it would have traversed a gravel desert 60 ft. across.

At 2 a.m., as soon as I had found the slug which had been under observation; upon a *Russula nigricans* fruit-body, I hunted carefully over the gravelled area for other slugs. I could find one more slug only—another *Limax maximus*—which had come out of the border and was heading straight for the row of fruit-body heaps from which it was only 8 ft. distant; but whether or not this second slug ever reached one of the heaps I cannot say, as at 2.5 a.m. I retired to bed and, in the morning, could not clearly distinguish the trail.

In the morning of September 12, I found that the slug which had visited the *Russula nigricans* fruit-bodies was no longer to be seen upon the gravel. Doubtless, it had once more retired to the border. It is doubtful whether the return journey could have been accomplished in less than two hours. It appears, therefore, that our *Limax maximus*, with the object of feeding upon a fungus and then returning home, must have spent some six or seven hours in a single night in wandering over the gravel where the fungus was. Such an effort shows how strongly fungi attract slugs of the *Limax maximus* species. Doubtless, the slugs in woods are also attracted to fungi from a distance of many feet. In view of my observations on *Limax maximus*, the success with which slugs in woods find out the fleshy Hymenomycetes can no longer be a matter for astonishment.

Experiment VII. On September 12, I made a fourth experiment with hymenomycetous fruit-bodies. On this occasion I used the *Russula nigricans* and *Cortinarius caninus* heaps alone, as the *Boletus scaber* fruit-bodies had now become thoroughly

decomposed. I set the two heaps of fruit-bodies on the gravel 4 ft. apart and each 21 ft. distant from the place in the border from which the slugs usually issued on their nocturnal forays; but the new position of the fungi was such that the slugs, if they sought the fungi, would be obliged to travel not in the direction taken during the previous two nights but in a direction making therewith an angle of 45° . The night was very still, and dark; there was no moon, and overhanging trees shut out from that part of the gravel which the slugs would be obliged to cross even the faint light of the stars. At 11.30 p.m., with the help of a taper, I found a slug moving toward the two heaps of fungi and only 9 ft. distant from them. It was a *Limax maximus*, exactly resembling the two I had seen the previous night, and its four horns were spread out in the air as though they were being used to detect the direction from which the odour of the fungi was coming. I could see by the slime-trail upon fallen leaves and gravel stones that the slug was making a gentle sweep toward the *Russula nigricans* fruit-bodies and that it had kept upon a steady course since it had left the border. Next morning, I found that the *Russula nigricans* fruit-bodies had been visited by two slugs during the night, for there were four slime-tracks passing between them and the border. Moreover, one large cavity and two smaller ones had been made by the slugs in one of the pilei. By careful tracking, I found that one of the slugs which we will assume was homeward bound, after feeding upon one of the *Russula nigricans* fruit-bodies, had made a détour and had visited the heap of *Cortinarius caninus* fruit-bodies. Here it had crept on to one of the pilei and tasted the gills, and then it had retired by a somewhat sinuous course to the border from which it had set out, 21 ft. away. The actual distance traversed by this slug in the course of its excursion to the two heaps of fungi must have been at least 50 ft.

The circumference of a circle with a radius of 21 ft. is 132 ft. The width of my heap of *Russula nigricans* fruit-bodies was 4 inches. Supposing, therefore, that the heap of fruit-bodies were on the circumference of a circle with a radius of 21 ft., as was actually the case in the experiment just recorded, and supposing, further, that a slug were to start from the centre of this circle and move at random radially outwards for a distance of 21 ft., the chances of the slug meeting the heap of fruit-bodies would be 395 to 1 against. Simple mathematical calculations of this kind afford strong evidence that the slugs in my experiments did not find the fungi in the night by chance but through the guidance of some stimulus coming from the fungi and received by their sense organs.

Immediately after making Experiment VII, I was obliged to leave England to return to my duties in Canada. My investigations upon the finding of fungi by slugs were thereby brought to an end.

SLUGS AND MUSTARD GAS.

There can be but little doubt that the stimulus which comes from the fungi to the slugs and which guides these animals on their foraging expeditions is gaseous in nature. It has been recently shown by Dr Paul Bartsch of the Smithsonian Institute, Washington, that *Limax maximus* is extraordinarily sensitive to certain gases. A few years ago a number of slugs of this species, which were under observation in his home, escaped from the box in which they had been confined. Their behaviour in the furnace room showed that they were sensitive to the fumes coming from the furnace and, in response thereto, made characteristic movements of their tentacles. After the United States entered the War and the need for a gas detector arose in connection with the fighting at the front, Dr Bartsch recalled his furnace-room observations. A very brief period of experimentation then revealed the extraordinary sensitiveness of *Limax maximus* to mustard gas, and such startling results were obtained that within two hours after the first experiment had been made, the Allied forces were advised by cable of the possibilities of using the slug as a gas detector. Dr Bartsch found that the tentacles of *Limax maximus* are sensitive to a dilution of 1 in 10,000,000 of mustard gas, and that they make characteristic responses indicating the degree of dilution. Dr Bartsch also found that man reacts to a dilution of 1 in 4,000,000. *Limax maximus*, therefore, is much more sensitive to the presence of mustard gas than man*. If *Limax maximus* is thus so extraordinarily sensitive to one gas, we have every reason for believing that it is extraordinarily sensitive to other gases, particularly those which emanate from its food substances such as fungi. If we assume such a sensitiveness, it is not difficult to imagine how it is that *Limax maximus* finds its way unerringly over a distance of many feet to the fruit-bodies of *Phallus*, *Boletus*, *Russula*, etc., which it devours with such avidity. The sense of smell in slugs, like that in dogs, is doubtless much more acute than in human beings.

* Paul Bartsch, Our Poison Gas Detector and How It was Discovered, Abstract of an Address delivered on Feb. 7, 1920, to the Biological Society of Washington, U.S.A. I read a paper entitled "Upon the Chemotactic Attraction of Fungi for Slugs" at Chicago on Dec. 30, 1920, before the Ecological Society of America. Subsequently Dr R. F. Griggs called my attention to Dr Bartsch's work, and then Dr Bartsch kindly sent me an abstract of his Address.

CONCLUSIONS.

(1) The successful experiments with *Phallus impudicus*, *Russula heterophylla* and *R. nigricans*, described above, clearly show that the fruit-bodies of these fungi, under certain conditions in the open, attract *Limax maximus* from a distance of at least 10 to 21 ft.

(2) Having regard to the well-known short-sightedness of slugs, to the fact that slugs find their food at night, and to the sensitiveness of *Limax maximus* to mustard gas when diluted to one part in ten million, my observations and experiments lead me to suppose that fungus-eating slugs react at a distance to the odours given off by fleshy fungi, and that in woods and gardens they find the fungi upon which they feed by their sense of smell.

(3) The chemotaxis of slugs, not merely for fungi but also for garden produce such as lettuce and cabbage, is a subject concerning which our information is still very meagre, but which is very amenable to experimental treatment. If the chemotaxis of slugs were sufficiently elucidated, we might perhaps be able to devise much more efficient means for protecting our gardens from the ravages of slugs than any at present known.

